

## THE COMPARATIVE MORPHOLOGY OF THE WINTERACEAE II. CARPELS

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*With six plates*

### INTRODUCTION

IN a previous paper, Bailey and Smith (1) called attention to the remarkable stamens and carpel of *Degeneria*, suggesting that they might prove to be of considerable significance in interpreting the floral morphology of the Ranales. In this genus of the monotypic family Degeneriaceae, both the stamens and the carpel appear to be primitive, palmately 3-veined sporophylls of but slightly modified form. The lamina of the megasporophyll is adaxially folded or conduplicate and bears numerous ovules on its morphological upper surface. In other words, the ovules are not attached to the margins of a classical, involute, sealed sporophyll, but to the ventral surface of the megasporophyll as in certain of the Pteridospermae.

Carpels of a fundamentally similar type occur in the *Tasmannia* section of *Drimys* and in certain species of *Bubbia*. Other representatives of the Winteraceae exhibit various trends of specialization in the modification of these primitive ranalian megasporophylls. The numerous species of the six genera of the family provide abundant material for comparative studies and demonstrate that the salient trends of specialization in the megasporophylls of the Winteraceae are unlike those which characterize the Magnoliaceae and the Himantandraceae (Bailey, Nast, and Smith, 2).

### MATERIAL AND METHODS

The herbarium specimens upon which our floral studies are based have been listed in Dr. Smith's papers (3, 4, 5) and need not be relisted here. The vascularization of carpels and other floral organs is commonly reconstructed by the laborious study of serial sections. We have found, however, that such investigations may be facilitated and much accelerated by carefully controlled clearing of flowers or parts of flowers. In the case of material from herbarium specimens, the following procedure is helpful and widely applicable to both flowers and leaves. The dry flowers or leaves are first heated in water until thoroughly saturated and freed of air. They are then transferred to a dilute aqueous solution of NaOH and placed in sealed bottles in an incubator at 55° C. until cleared to the desired degree. They are next washed free of NaOH and transferred to vials of 95% alcohol for visual study. Permanent mounts can be made by passing the material through absolute alcohol, diaphane solvent to diaphane or through absolute alcohol, toluene to clarite. The clarity of the vascularization depends upon the refractive index of the medium and the consistency of the tissues.



Commonly the venation shows best in alcohol, and the unmounted specimens may be turned for examination at all angles. Staining of the material is unnecessary either for visual examination or for photomicrography. The method is adequate except in cases where organs are excessively hairy or where they contain numerous clusters of sclereids, as in the floral parts of certain species of *Bubbia*, *Exospermum*, and *Zygogynum*. In dealing with such material, one is forced to rely largely upon serial sections.

#### CARPELS OF THE TASMANNIA SECTION OF DRIMYS

There is a conspicuous tendency in many ranalian families for the leaves to be adaxially folded or conduplicate during the earlier stages of their ontogenetic development. In such species of the *Tasmannia* section of *Drimys* as *D. piperita* Hook. f., the carpels resemble in external form these conduplicate young leaves. There is a similar differentiation of the megasporophylls into stipe (petiole), *Fig. 1*, and conduplicate lamina, compare *Figs. 1* and *12*. The more or less closely approximated ventral surfaces<sup>1</sup> of the conduplicate megasporophyll frequently are not extensively and firmly concrescent prior to and during anthesis. Thus, the conduplicate lamina may be spread open without serious or extensive rupture and distortion of the carpel or of its constituent tissues, *Fig. 17*.

The carpels are vascularized by three veins, a median vein and two lateral veins. The median vein frequently bifurcates and has numerous conspicuous branches of considerable length, *Fig. 17*. The two lateral veins commonly have short branches that are directed both outward toward the margins of the megasporophyll and inward toward the branches of the median vein, *Figs. 1* and *3* and left half of *Fig. 17*. In certain cases, the lateral veins have extensive branches that run parallel to them, right half of *Fig. 17*. The ovules are remote from the margins of the megasporophyll and are invariably attached between the median and the lateral veins, i.e. in the parts of the carpel where the branches of the median and lateral vascular systems tend to overlap and anastomose. The ovules are vascularized in part by extensions of the veinlets of the lateral systems (*a* in *Figs. 17* and *18*), in part by extensions of the veinlets of the median system (*b* in *Figs. 17* and *18*), and in part by strands arising from anastomosed

<sup>1</sup>In order to avoid confusion in morphological descriptions, it is essential to recognize that the terms ventral and dorsal are used in two distinct ways, (1) in referring to the upper and lower *surfaces* of flat, cladified appendages, and (2) in designating *parts* or sides of folded megasporophylls, viz. carpels. There are ontogenetic and phylogenetic implications in both usages.

We shall refer to the upper or morphologically adaxial surface of leaves and sporophylls as ventral, to the lower or morphologically abaxial surface as dorsal. In conduplicate ranalian carpels, the exposed outer surfaces are, therefore, dorsal and the internal ones ventral.

In dealing with conduplicate ranalian carpels, we shall refer to the primitively abaxial part of the sporophyll (the part vascularized by the median vein) as dorsal, to the primitively adaxial parts (those vascularized by the lateral veins) as ventral. In unmodified conduplicate carpels, the ventral parts are adaxially oriented, *Fig. 1*, whereas in certain specialized forms, *Figs. 20-23*, their actual orientation may be in part terminal or even abaxial.



branches of the median and lateral systems (*c* in *Figs. 17* and *18*). The details of the vascularization, both of the carpels and of the ovules, fluctuate considerably from carpel to carpel of the same species and of the same flower. Thus, the ovules may be vascularized at times largely by the median system, by the lateral systems, or by varying combinations of these systems.

As shown in *Fig. 12*, the free margins of the conduplicate megasporophylls are provided with conspicuous, glandular-appearing, papillate cells or hairs, which extend backward from the margins for varying distances over the exposed dorsal surfaces of the conduplicate megasporophylls. That the papillae are glandular and function as a stigmatic surface is demonstrated by adhering pollen at anthesis, *Fig. 2*, and by pollen-tubes which penetrate the mat of papillae. Thus, the carpels are provided with extensive stigmatic crests (actually double), which extend from the region of the stipe along the conduplicate adaxial parts of the sporophyll and slightly overtop its apex, *Figs. 1* and *2*.

The fertile carpels have a fundamentally similar conduplicate form, placentation, and vascularization throughout the 15 species of the *Tasmannia* section of *Drimys* that we have studied. There are variations in the length of the stipe, in the size and form of the conduplicate lamina, in the extension of the outer stigmatic surfaces, in the concrescence of the approximated ventral surfaces, in the number and form of the ovules, and in the details of the vascularization, but only in two of the investigated species are the deviations of considerable magnitude. The carpels of *D. stipitata* Vickery are characterized by their excessively elongated stipe; those of *D. lanceolata* (Poir.) Baill. by their unusually fleshy conduplicate lamina of nearly globular form, *Fig. 27*.

The sterile megasporophylls of staminate flowers usually are smaller, but they have a similar conduplicate, palmately 3-veined lamina, *Fig. 2*. Although no ovules are formed, the stigmatic surfaces are conspicuously developed and are encrusted with firmly adherent pollen at anthesis, *Fig. 2*. In the more rudimentary forms of sterile carpels, the branches of the median and lateral veins may be feebly developed or absent, thus resembling the venation of fertile carpels during the earlier stages of their ontogeny.

#### CARPELS OF THE WINTERA SECTION OF DRIMYS

In the *Tasmannia* section of *Drimys*, the carpels are adaxially folded or conduplicate and may be spread open into megasporophylls of but slightly modified form. When unfolded, *Fig. 17*, their venation resembles that of a palmately 3-veined appendage. The elongated locule of the folded carpel is oriented approximately parallel to the long axis of the megasporophyll, and the numerous ovules are attached to two placental ridges that are situated between the median and lateral veins.

The carpels throughout the *Wintera* section of *Drimys* have a fundamentally similar vascularization and placentation, but the external stigmatic surfaces are restricted to the adaxially projecting, subapical, ventral part of the carpels, *Fig. 6*. The approximated ventral surfaces of the condupli-



cate carpels are firmly concrescent, *Fig. 14*, except at the level of the stigmatic projection, *Fig. 13*, and therefore the megasporophylls cannot be unfolded as in the case of the more primitive sporophylls of the *Tasmannia* type. At the level of the stigmatic projection, *Fig. 13*, there is a cleft-like opening or a loose suture which extends outward from the locule as in *Drimys piperita*, *Fig. 12*, of the *Tasmannia* section of *Drimys*. Serial transverse sections indicate that the closure of the carpels progressed upward from the base and downward from the apex of the conduplicate lamina, and commonly also centripetally, since vestiges of the cleft-like opening tend to persist internally, *Fig. 14*, after they have been completely eliminated externally. These conclusions regarding closure may be verified by the serial sectioning of *Tasmannia* type carpels, many of which exhibit incipient stages of concrescence. With the closure of the cleft-like opening, the carpels retract, and eventually eliminate, the stigmatic crests from the sealed parts of the megasporophylls. Thus, the subapical projection of the *Wintera* type of carpel is not to be interpreted as a style-like outgrowth, but rather as a persistent remnant of the extensive adaxial stigmatic crests of *Tasmannia* type megasporophylls, *Fig. 19*.

#### CARPELS OF BUBBIA, BELLIOLUM, EXOSPERMUM, AND ZYGOGYNUM

Various transitional stages in the closure of conduplicate carpels and in the restriction of their stigmatic crests occur in the genus *Bubbia*, but in this genus, as in *Belliolum*, *Exospermum*, and *Zygogynum*, there is in addition a more or less pronounced abaxially directed deformation of the conduplicate megasporophylls.

The carpels of *Bubbia Archboldiana* A. C. Sm. (*Brass* 12712) resemble those of the *Tasmannia* section of *Drimys* in their vascularization, placentation, and in having extensive stigmatic surfaces, *Fig. 20*. They differ in their angular external form and in their conspicuously broadened and flattened apices. There are, however, no significant modifications in the longitudinal orientation of the locule, the placental ridges, or the median and lateral veins. The carpel of *Bubbia megacarpa* A. C. Sm. (*Brass* 10249) likewise has extensive stigmatic margins, *Fig. 21*, but it exhibits a profoundly modified form, due to the overtopping of the shortened dorsal side of the sporophyll by its over-extended, conduplicate, ventral side. In other words, there is an abaxially directed deformation of the megasporophyll which produces a short, apically much broadened carpel. The locule, the placental ridges, the lateral veins, and the stigmatic crests all show pronounced abaxial curvatures. Owing to these concomitant deformations from longitudinal to approximately transverse orientations, it is evident that the apparently terminal parts of the carpel, *Fig. 21*, actually are homologues of the ventral parts of the primitive carpels illustrated in *Fig. 1*. The true apex of the carpel is curved around onto the dorsal side of the megasporophyll. The massive median trace dissociates in the base of the carpel, *Fig. 21*, into numerous vascular strands, the majority of which extend upward toward the transversely oriented parts of the placental ridges. Their recurved ends either terminate in the placental ridges or



anastomose with the short downwardly directed branches of the lateral veins. Comparatively few branches of the median vein are directed diagonally toward the longitudinally oriented basal parts of the placental ridges. Most of the ovules are vascularized by veinlets of the lateral systems.

The carpels of other species of *Bubbia*, as of *Belliolum* and *Zygogynum*, exhibit more or less conspicuous abaxially directed deformations and, in addition, much restricted stigmatic crests which tend to assume a transversely terminal orientation. Although the carpels of *Bubbia longifolia* A. C. Sm. (*Brass* 13868) have less exaggerated abaxial deformation, *Figs.* 10 and 22, and therefore a less modified median vein than that of *B. megacarpa*, *Fig.* 21, the stigmatic crests and the ovules are restricted to the diagonal upper part of the distorted megasporophylls. The approximated ventral surfaces in the lower ventral part of the conduplicate carpel are concrescent and there is no cleft-like opening extending outward from the locule except in the upper part of the megasporophyll which subtends the stigmatic crests. The placental ridges and ovules are likewise restricted to the upper part of the sporophyll. The ovules are vascularized in part by veinlets of the lateral systems and in part by extensions of the median system, *Fig.* 22. The single, terminal megasporophyll of *Bubbia monocarpa* A. C. Sm. (*Kanehira & Hatusima* 12105), *Fig.* 9, resembles the carpels of *B. longifolia* both in its abaxial deformation and its internal structure. It demonstrates, as does the single terminal carpel of *B. megacarpa*, that the distorted forms of the megasporophylls in polycarpellate species are not due solely to excessive compression of adjacent organs during ontogenetic development. The immature carpels, illustrated in *Figs.* 7 and 8, indicate furthermore that the abaxial deformations are of phylogenetic rather than purely ontogenetic development.

In *Bubbia Clemensiae* A. C. Sm. (*Clemens* 5157 and 4596), abaxial deformation coupled with concomitant modifications of the lower part of the megasporophylls have produced a more nearly symmetrical carpel, *Fig.* 23. Externally it is difficult to distinguish the sealed, crestless, adaxial side of the conduplicate sporophyll from its dorsal side. Furthermore, the lateral veins not infrequently are fused in the lower closed part of the carpel and separate at a higher level, thus simulating the bifurcation of the median vein. The transversely oriented placental ridges extend downward into the locule for a considerable distance, *Fig.* 15. Therefore, the attachment of the ovules is more remote from the stigmatic margins and the ovules are vascularized by more downwardly extended veinlets of the lateral and median systems.

The carpels of *Bubbia Whiteana* A. C. Sm. (*Brass* 2278), *Figs.* 11 and 24, resemble the megasporophylls of *B. Clemensiae* in their concealed abaxial deformation and in their much modified median and lateral vascular systems, but differ from them in having less extensive terminal stigmatic crests and ovules that are attached at a higher level of the locule. The ovules, as in *B. Clemensiae*, are vascularized by extensions of both the lateral and median systems.



Restriction of the stigmatic crests is carried to an extreme in the short, terminally broadened, fleshy carpels of *Bubbia auriculata* v. Tiegh. (Vieillard 2280) and *B. semecarpoides* (F. v. Muell.) Burt (Kajewski 1216). There is a pronounced abaxially directed deformation in the ventral part of the conduplicate carpel, as indicated by the curvature of the lateral veins and the diagonal orientation of the placental ridges, Fig. 25, but the conduplicate ventral part of the carpel does not extend across the broad terminal face of the megasporophyll and does not overtop a shortened dorsal side as in *B. megacarpa*, Fig. 21, or *B. Clemensiae*, Fig. 23.

In most species of *Bubbia*, as in the *Tasmannia* section of *Drimys*, the placental ridges are closely correlated in orientation and extension with the stigmatic crests. In certain carpels, however, e.g. those of *B. pachyantha* A. C. Sm. (Brass 4371) and *B. isoneura* v. Tiegh. (Vieillard 17), there are more or less conspicuous unconformities, as in the megasporophylls of the *Wintera* section of *Drimys*, Fig. 19. In other words, the placental ridges persist for varying distances in the sealed, crestless, ventral part of the megasporophylls. Such unconformities between the orientation and extension of the placental ridges and the stigmatic crests occur at times in the carpels of *Belliolum*, Fig. 26. Although the carpels of *Belliolum* in general resemble those of the more highly specialized species of *Bubbia* (viz. those having more or less restricted, terminally oriented crests), the attachment of the ovules tends to be at lower levels and the branches of the lateral veins are more downwardly extended, as in *Bubbia Clemensiae*, Fig. 23.

The coriaceous megasporophylls of certain polycarpellate species of *Bubbia*, e.g. *B. pachyantha*, are closely crowded and firmly coherent both preceding and during anthesis. Thus, as stated by Smith (3), "the gynaecium has the appearance of a compound ovary with a 3- or 4-parted stellate stigma." Such gynaecia closely resemble that of *Exospermum stipitatum* (Baill.) v. Tiegh. (Vieillard 2281). There is, accordingly, no such sharply defined morphological distinction between coherent (*Exospermum*) and free (*Bubbia*) carpels as hypothesized by van Tieghem (6). The individual carpels may be readily separated after clearing treatments and each is provided with an independent epidermal layer. Only in the gynaecia of *Zygogynum* are the carpels fused into a concrescent mass without internal evidences of sutures, Fig. 16.

The ovules of *Exospermum stipitatum* are not restricted in their attachment to conspicuous stigmatic ridges, but are scattered over the walls of the locule, a modified type of placentation that is suggestive of certain Nymphaeaceae and Lardizabalaceae. The cleft-like opening at anthesis is partly closed externally and does not extend outward from the locule to the stigmatic surface as in *Zygogynum spathulatum* v. Tiegh. (Vieillard 2266), Fig. 16. In this, as in other species of *Zygogynum*, the shortened placental ridges, Fig. 16, are situated on the abaxial side of the locule. The ovules are not attached to the dorsal part of the carpel, however, as hypothesized by van Tieghem (6), but to a morphologically ventral part of the conduplicate megasporophylls that has been deflected into an



abaxial orientation and thus overtops the much shortened morphologically dorsal part of the carpel.

The carpels of *Pseudowintera* fluctuate considerably in form. In general, those of *P. axillaris* var. *colorata* (Raoul) A. C. Sm., *Fig. 4*, tend to resemble the megasporophylls of the *Wintera* section of *Drimys*, whereas those of *P. axillaris* var. *typica* A. C. Sm., *Fig. 5*, exhibit more pronounced abaxially directed deformation as in certain species of *Bubbia*.

#### SIGNIFICANCE OF INTERNAL PAPILLATE SURFACES

The conduplicate megasporophylls of *Degeneria* (Bailey and Smith, 1) have more or less conspicuously flaring free margins and are characterized by having short, glandular-appearing hairs that are distributed inwardly from the margins along the approximated ventral surfaces as far as the flanks of the placental ridges. Thus, the cleft-like opening that extends outward from the locule is partly occluded by interlocking papillae, and pollen does not have direct access to the locule in most cases. The pollen grains become attached to the outer glandular projections and the pollen-tubes penetrate apparently through the mat of interlocking papillae.

In the Winteraceae, the free margins of the conduplicate lamina (in unsealed parts of the carpels) are more closely approximated and the stigmatic papillae extend backward from the margins over the exposed dorsal surfaces of the sporophylls, *Figs. 12* and *13*. There are, in addition, more or less numerous papillate cells along the ventral surfaces of the conduplicate megasporophylls, *Figs. 12* and *13*. These projecting cells commonly jacket both flanks of the placental ridges even in sealed parts of the carpels, *Fig. 14*. In regions of incipient closure (phylogenetic, not ontogenetic) the papillae not infrequently appear to enlarge and to interlock and possibly at times to play an initial role in the developing suture.

Unfortunately, herbarium specimens do not provide adequate material for studying the finer cytological and histological details of the closure of carpels or of the penetration of pollen-tubes. Such details can be clarified only by the study of living and adequately killed and fixed material. Furthermore, it is essential that the carpels of *Degeneria* and the Winteraceae be studied in all stages of their ontogenetic development and during the changes that they undergo subsequent to anthesis.

It should be emphasized in this connection that there is considerable variation in the form of winteraceous carpels, in the details of their vascularization, in the extent of their closure, etc., not only in material from different collections of the same species, but also in different carpels from the same flower. Therefore, our descriptions and illustrations represent average or typical conditions. Numerous variations in the structural details of particular genera and species may be anticipated when more abundant and complete collections of these remarkable plants become available.

#### DISCUSSION AND CONCLUSIONS

The carpels of the *Tasmannia* section of *Drimys* are conduplicate megasporophylls of but slightly modified form and closely resemble the mega-



sporophyll of *Degeneria*. In both cases, the megasporophyll is clearly differentiated into stipe and adaxially folded lamina, *Figs. 1 and 2*. When spread open, the lamina exhibits a palmately 3-veined vascularization such as characterizes both the microsporophylls and the sterile sporophylls (staminodes) of the Degeneriaceae and Himantandraceae. The numerous anatropous ovules, *Fig. 18*, are attached to more or less conspicuous placental ridges that are situated between the median and the lateral veins, *Fig. 17*. The ovules are vascularized in part by short branches of the two lateral veins, in part by branches of the median vein, and in part by strands originating near anastomoses of the lateral and median vascular systems, the ratios of the three types of vascularization fluctuating from carpel to carpel. The conduplicate form, placentation, and vascularization of the megasporophyll do not conform with the classical interpretation of the angiosperm carpel as an involute megasporophyll bearing marginally attached ovules. In the Winteraceae and Degeneriaceae, the ovules are borne on the morphological upper surface of the megasporophyll, *between the lateral and median veins, Fig. 17*, and remote from the margins of the sporophyll, *Figs. 12, 13, 15, and 16*. It should be noted in this connection that the broad, palmately 3-veined microsporophylls of the Degeneriaceae and Himantandraceae are not differentiated into filament, anther, and connective, and that they bear four slender elongated sporangia that are immersed beneath the dorsal surface of the sporophyll, *midway between the median and the lateral veins*. Thus, in these primitive ranalian carpels and stamens, neither the megasporangia nor the microsporangia are borne upon the margins of the sporophylls. It should be noted, in addition, that there is no conclusive evidence at present for inferring marginal attachments in ancestral angiosperms rather than ventral and dorsal ones as in certain of the Pteridospermae.

In the Winteraceae, the chief trends of specialization of the primitive ranalian megasporophyll lead toward closure of the conduplicate sporophyll (by concrescence of its approximated ventral surfaces) and concomitant restriction of its external stigmatic surfaces. In *Bubbia*, *Bellium*, *Exospermum*, and *Zygogynum* these trends of specialization are complicated by more or less pronounced abaxially directed deformation which results in an apically much broadened carpel bearing more or less terminally or even abaxially (*Zygogynum*) oriented stigmatic crests. In the more specialized forms, the ovules tend to be attached to transversely or even abaxially oriented placental ridges in the upper part of the carpel.

On the contrary, in the Himantandraceae and Magnoliaceae (the closest relatives of the Degeneriaceae) the specializations of the primitive ranalian megasporophyll lead toward a pronounced constriction of the upper part of the conduplicate lamina. This constricted, sterilized, upper part, viz. style, has more or less extensively "decurrent" stigmatic surfaces and still exhibits a conduplicate structure. The few remaining ovules are thus confined to the fertile, lower, broader part of the conduplicate carpels, which may remain partly open (Himantandraceae) or be firmly sealed (Magnoliaceae).



Our detailed investigations of the numerous representatives of the Winteraceae support the suggestion (Bailey and Smith, 1) that the remarkable megasporophyll of *Degeneria* may afford significant clues for interpreting the diverse carpellary structures of the Ranales. The occurrence of fundamentally similar types of conduplicate megasporophylls throughout the *Tasmannia* section of *Drimys* provides a broad basis for comparative investigations of the various ranalian families. If the dicotyledons are monophyletic, the megasporophylls of the Degeneriaceae and Winteraceae should prove to be equally significant in studying the carpellary specializations of other orders.

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#### EXPLANATION OF PLATES

##### PLATE I

Carpels cleared in dilute NaOH and photographed unstained in 95% alcohol. FIG. 1. *Drimys piperita* Hook. f., Ramos and Edaño 38897. Two attached carpels, showing stipe and venation of conduplicate lamina,  $\times 20$ . FIG. 2. *Drimys macrantha* A. C. Sm., Brass 4519. Detached sterile carpel, showing at right pollen attached to stigmatic surface,  $\times 24$ . FIG. 3. *Drimys insipida* (R. Br.) Pilger, Caley. Detached young fruit, showing at left outwardly projecting branches of lateral vein,  $\times 17$ .

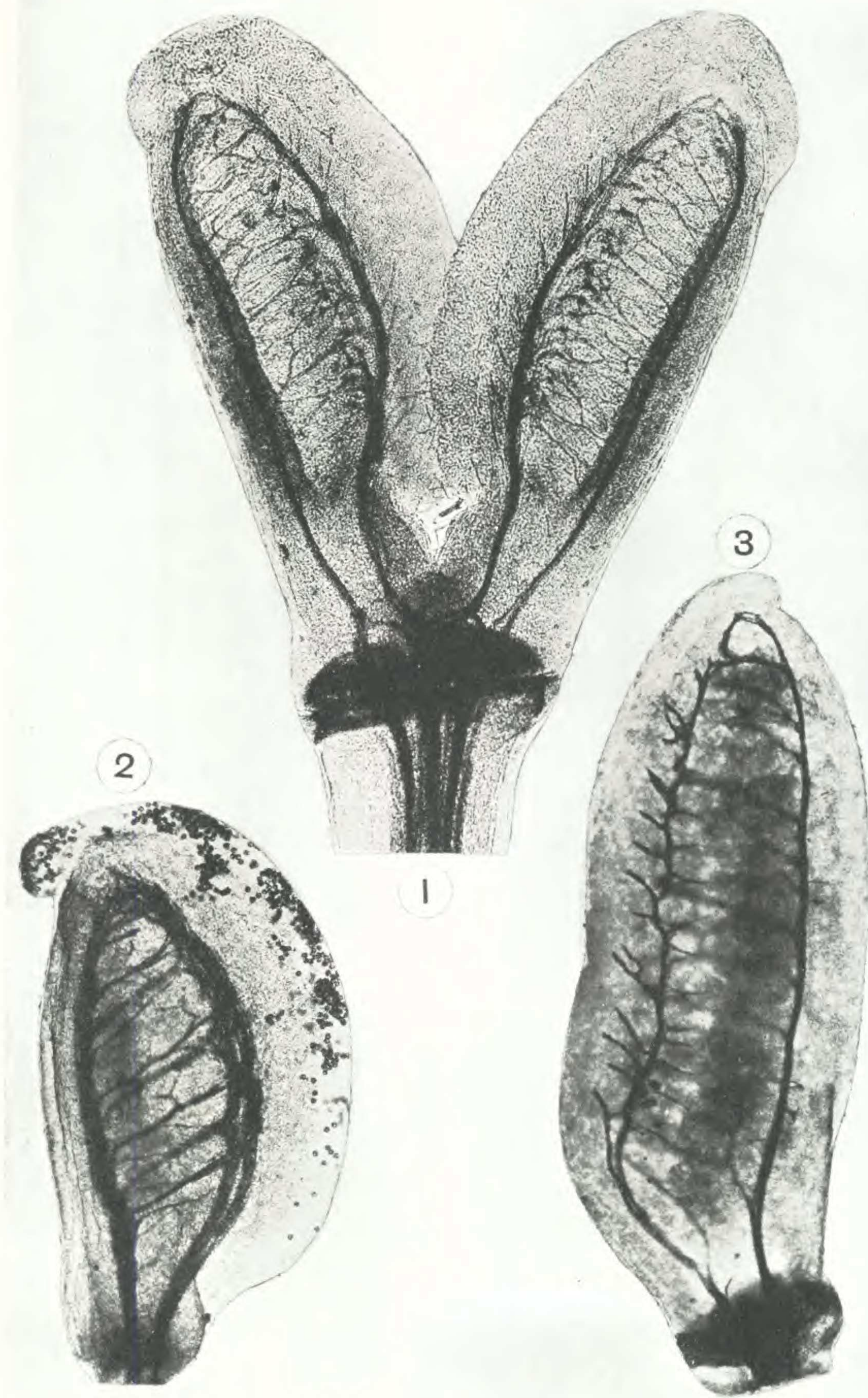
##### PLATE II

Carpels cleared in dilute NaOH and mounted unstained in diaphane. FIG. 4. *Pseudowintera axillaris* var. *colorata* (Raoul) A. C. Sm., Kirk. Two attached carpels, showing lateral view of vascularization,  $\times 24$ . FIG. 5. *Pseudowintera axillaris* var. *typica* A. C. Sm., Oliver. Two attached carpels, showing lateral view of vascularization,  $\times 20$ . FIG. 6. *Drimys confertifolia* Phil., Moseley. Two attached carpels, showing vascularization and apex of torus,  $\times 20$ .

##### PLATE III

Carpels cleared in dilute NaOH and photographed unstained in 95% alcohol. FIG. 7. *Bubbia monocarpa* A. C. Sm., Kanehira and Hatusima 12105. Young carpel, showing early stage in the development of median and lateral veins,  $\times 24$ . FIG. 8. *The same*. Somewhat older carpel, showing extensions of the vascularization,  $\times 24$ . FIG. 9. *The same*. Carpel showing vascularization at anthesis,  $\times 24$ . FIG. 10. *Bubbia longifolia* A. C. Sm., Brass 13868. Mature detached carpel, showing vascularization,  $\times 24$ . FIG. 11. *Bubbia Whiteana* A. C. Sm., Brass 2278. Two somewhat coherent carpels, showing vascularization,  $\times 17$ .





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